

found in any of the habitats, and zygote diameters and capsular periods did not overlap (Table 1).

The dichotomous nature of these characteristics suggests that *D. frondosus* has limited phenotypic plasticity with regard to larval feeding type. In one of the clearest examples of poecilogony, Krug (1998) found mixed clutches of lecithotrophic and planktotrophic larvae in populations of the ascoglossan opisthobranch *Alderia modesta*. Other cases of poecilogony have documented geographically separated populations of a species with different larval types where the adults can interbreed (Levin, 1984; West et al., 1984). The lack of mating recognition between individuals from the populations of *D. frondosus* described in this paper (Table 2) appears to preclude this type of poecilogony.

Quality of adult diet and feeding history has been shown to be an important factor resulting in shifts in larval type for poecilogonous species (Krug, 1998) and changes in capsular period (Gibson & Chia, 1995; Chester, 1996). In this study, reciprocal feeding experiments with adults fed the lower quality diet of *Sertularia* spp. from intertidal habitats and the higher quality *Obelia* spp. from subtidal habitats did not result in any differences in the resulting larval type. Higher growth rates were measured for both types of *D. frondosus* when fed *Obelia* spp., and a high level of mortality was recorded for the *Sertularia* treatment group, especially for the southern subtidal trial. Reduced production of spawn masses on a lower quality diet (*Sertularia* spp.) indicates some gross changes in reproductive effort. Unfortunately, zygote diameters were not measured in these experiments, nor were there any direct measurements of reproductive output in response to these treatments. However, the lack of shift in larval feeding types in response to adult diets of differing quality suggests that this remains a fixed trait for these nudibranch types, and poecilogony is unlikely for *D. frondosus* in the Gulf of Maine. It is important to note here the variation in diameters of zygotes from animals collected in the field despite the consistent disparity between feeding requirements of the resultant larvae (Table 1). Although these life history patterns are dichotomous, there may be considerable variation surrounding each developmental mode. Still, there appears to be little evidence for poecilogony for *D. frondosus* in the Gulf of Maine.

Given the differences in larval type and seasonal patterns of adult occurrence, the separation of populations of this species may not be explained simply by phenotypic plasticity of reproductive traits. This study also evaluated the potential for mating behavior between adults in the northern intertidal and southern subtidal populations. Other mating recognition studies have been used to help clarify sibling species complexes and indicate a strong possibility for reproductive isolation between the two most extreme groups (Hirano & Hirano, 1991; Langan-Cranford & Pearse, 1995). *Dendronotus frondosus*

adults collected from northern intertidal and southern subtidal sites in the Gulf of Maine do not recognize each other as potential mates, representing a distinct reproductive isolation mechanism between these two populations. Only a limited number of replicates from northern subtidal populations were attempted and these yielded similar results by dividing the two reproductive patterns. These data also suggest that the northern subtidal habitat may support sympatric populations of the two types of *D. frondosus* corresponding with the presence of both planktotrophic and lecithotrophic larvae.

The division of life history patterns, larval morphology, and mating recognition behavior is motive for a formal taxonomic review of *D. frondosus* in the Gulf of Maine. This review should include molecular genetic data, comparisons of the radula and reproductive system, and a thorough reanalysis of the literature for the history of this genus in the north Atlantic.

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A New Species of *Granigyra* Dall, 1889 (Gastropoda: Skeneidae) from Brazil and a Review of Known Western Atlantic Species

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Abstract. *Granigyra oblatogyra*, sp. nov. is described based on the shell morphology of seven individuals collected between 510–1250 m off the Brazilian coast. It is characterized by its apically flattened whorls and anteriorly projected aperture. A brief review of the three previously known west Atlantic species is presented. The lectotype of *G. radiata* Dall, 1927, (herein designated), and the holotype of *G. spinulosa* (Bush, 1897) are illustrated by SEM for comparison with the new species.

INTRODUCTION

The genus *Granigyra* Dall, 1889, comprises a group of minute, trochoid “skeneimorph” gastropods characterized by a sandlike granulation on the shell surface. They are known only from bathyal and abyssal depths, and species are reported primarily from the Atlantic ocean, with a single species from Sumatra (Warén, 1992, 1993). In the western Atlantic, there are species described: *G. radiata* Dall, 1927, from Florida, USA; *G. spinulosa* (Bush, 1897), from the Bahamas; and *G. limata* (Dall, 1889), from Cuba.

The taxonomic position of the genus *Granigyra* is controversial. Hickman & McLean (1990) and Hickman (1998) treated Skeneidae as a polyphyletic assemblage of minute-shelled, non-nacreous taxa of widely differing radular morphology, where many genera might reside provisionally. Warén (1992) adopted a more narrow definition that included a turbinid-like radula and the presence of a unique propodial penis. Although Warén (1992, 1993) found these features lacking in *Granigyra*, he retained the genus provisionally in Skeneidae. In the present study, we follow this provisional classification.

Herein we describe a new species of *Granigyra* collected by dredging carried out during oceanographic expeditions along the Brazilian coast. This is the first record of this genus from Brazilian waters, and review of the other western Atlantic species. In the description section, diameter and number of protoconch whorls were measured following Leal (1991).

Abbreviations used through the text: ANSP—Academy of Natural Sciences of Philadelphia, Philadelphia; IB-UFRJ—Instituto de Biologia/Universidade Federal do Rio de Janeiro, Rio de Janeiro; JOPS—Joint Oceanographic Projects, Research Vessel *Victor Hansen* coll; MNHN—Muséum National d’Histoire Naturelle, Paris; MNRJ—Museu Nacional/Universidade Federal do Rio de Janeiro, Rio de Janeiro; MORG—Museu Oceanográfico

“Eliézer de Carvalho Rios,” Rio Grande; MZSP—Museu de Zoologia da Universidade de São Paulo, São Paulo; PUC—Pontifícia Universidade Católica do Rio de Janeiro, Rio de Janeiro; USNM—National Museum of Natural History, Washington, DC; YPM—Peabody Museum of Natural History/Yale University, New Haven.

SYSTEMATICS

[?] Family SKENEIDAE Clark, 1851

Genus *Granigyra* Dall, 1889

Type species by monotypy *Cyclostrema*
(*Granigyra*) *limatum* Dall, 1889

Granigyra oblatogyra de Souza & Pimenta,
sp. nov.

Figures 1–4

Type material: Holotype: MNRJ 8433, off Rio Doce, Espírito Santo State (JOPS #3228: 19°45.5'S, 038°45.8'W, 1100 m), length: 2.5 mm, width: 2.4 mm; paratypes: USNM 894863 (JOPS #3228: 19°45.5'S, 038°45.8'W, 1100 m), length: 1.5 mm, width: 1.4 mm; IBUFRJ 11019, off Macaé, Rio de Janeiro State (22°41'25.36"S, 040°26'49.19"W, 780 m), length: 2.3 mm, width: 2.2 mm; MNHN, off Rio Doce, Espírito Santo State (JOPS #3221: 19°50.6'S, 039°34.8'W, 510 m), length: 1.6 mm, width: 1.5 mm (lip broken); ANSP 407933, off Macaé, Rio de Janeiro State (22°37'48.62"S, 043°22'50.14"W, 720 m), length: 2.0 mm, width: 2.0 mm (protoconch broken); MORG 41034, off Macaé, Rio de Janeiro State (22°37'48.62"S, 043°22'50.14"W, 720 m), length: 1.5 mm, width: 1.4 mm; MZSP 32870, off Macaé, Rio de Janeiro State (22°36'52.65"S, 040°40'25.25"W, 1250 m), length: 1.6 mm, width: 1.6 mm.

Type locality: off Rio Doce, Espírito Santo State (JOPS #3228: 19°45.5'S, 038°45.8'W, 1100 m), Brazil.

Range: Espírito Santo State to north of Rio de Janeiro State, Brazil.

Diagnosis: Species with apically flattened whorls and anteriorly projected aperture.

Description: Shell medium sized for the genus (holotype: length: 2.5 mm; width: 2.4 mm), turbiform. Surface white, covered with somewhat coarse granulation. Granules increasing in size, following the growth of the shell, resembling striated mountain peaks with flat tops, and much smaller granules in between them (Figure 2). Protoconch (Figure 4) small (diameter: about 220 μm), covered with very fine irregular granules, with about one whorl. Teleoconch with 2.5 distinctively rounded, posteriorly flattened whorls that increase rapidly in diameter; connection with previous whorls narrow. Aperture rounded, holostomate, slightly elliptical, projecting slightly anteriorly, with a flat, posterior shoulder next to suture. Umbilicus narrow, slitlike, deep.

Etymology: This species is named after its posteriorly flattened whorls (*oblata* = flattened at the poles; *gyra* = turn).

Granigyra limata (Dall, 1889)

Cyclostrema (*Granigyra*) *limatum* Dall, 1889:395 [holotype: USNM 214280, Blake sta. 19, off Bahia Honda, Cuba].
Granigyra limata (Dall, 1889): Dall, 1927:123; Abbott, 1974:56; Warén, 1992: 175, fig. 31E.
Lissospira (*Ganesa* sect. *Granigyra*) *limata* Bush, 1897: 135.

Granigyra spinulosa (Bush, 1897)

(Figures 5, 6)

Lissospira (*Ganesa* sect. *Granigyra*) *spinulosa* Bush, 1897: 135 [holotype: YPM 15805, USFC sta. 2655 (27°22'N, 078°07'30"W)].
Granigyra spinulosa (Bush, 1897): Abbott, 1974:56; Johnson, 1989:65, pl. 10 fig. 1.

Granigyra radiata Dall, 1927

(Figures 7, 8)

Granigyra radiata Dall, 1927:123 [lectotype: USNM 108138, off Fernandina, Florida (herein designated)]; Abbott, 1974:56; Warén 1992: 175, fig. 31E.

Remarks: We designate the lectotype of *G. radiata*, as the genus *Granigyra* comprises small somewhat similar

species that may lead to confusing identifications. The species is illustrated for the first time.

Discussion: See Warén (1992) for synonymy and taxonomic discussion of the genus.

Granigyra oblatogyra has ellipsoid, and posteriorly flattened whorls that distinguish it from *G. limata* (holotype figured in Warén, 1992:232, fig. 31E) that also has much coarser granulation on the body whorl.

The higher shell profile and the ellipsoid, posteriorly flattened whorls of *G. oblatogyra* distinguish it from *G. spinulosa* (Figures 5, 6). In *G. spinulosa* the contact between whorls is wider, and the umbilicus is wider than in *G. oblatogyra*.

Granigyra oblatogyra has more convex whorls, a deeper suture, and thinner granulation than *G. radiata* (Figures 7, 8). *Granigyra radiata* also has coarse granules irregularly fused into radially oriented ridges almost parallel to growth lines (Figures 7, 8).

In addition to the western Atlantic species, there are four species in the eastern Atlantic, and one from Sumatra (Warén, 1992, 1993). The most similar to *G. oblatogyra* is *G. granulifera* Warén, 1992:236, figs. 35A–E, but it differs by its nearly to totally disjunct whorls, lower profile, and thinner, less dense granulation.

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Figures 1–8. Figures 1–4. Holotype of *Granigyra oblatogyra* de Souza & Pimenta, sp. nov. Figure 1. Apertural view (length: 2.7 mm; width: 2.4 mm). Figure 2. Detail of sculpture, scale 50 μm . Figure 3. Ventral view. Figure 4. Detail of protoconch, scale 50 μm . Figures 5, 6. Holotype of *Granigyra spinulosa* Bush, 1897. Figure 5. Apertural view (length: 2.3 mm; width: 2.2 mm). Figure 6. Detail of protoconch, scale 50 μm . Figures 7, 8. Lectotype of *Granigyra radiata* Dall, 1927. Figure 7. Apertural view (length 2.0 mm; width: 1.9 mm). Figure 8. Dorsal view, showing protoconch and radial sculpture.